NeoBiota 32: 1–20 (2017)
doi: 10.3897/neobiota.32.10199
http://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Troubling travellers: are ecologically harmful alien species associated with particular introduction pathways?

Jan Pergl[1], Petr Pyšek[1,2,3], Sven Bacher[4], Franz Essl[5], Piero Genovesi[6], Colin A. Harrower[7], Philip E. Hulme[8], Jonathan M. Jeschke[9,10,11], Marc Kenis[12], Ingolf Kühn[13,14,15], Irena Perglová[1], Wolfgang Rabitsch[16], Alain Roques[17], David B. Roy[7], Helen E. Roy[7], Montserrat Vilà[18], Marten Winter[15], Wolfgang Nentwig[19]

1 *Institute of Botany, Department of Invasion Ecology, The Czech Academy of Sciences, CZ-252 43 Průhonice, Czech Republic* **2** *Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Prague, Czech Republic* **3** *Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland 7602, South Africa* **4** *University of Fribourg, Department of Biology, Chemin du Musée 10, 1700 Fribourg, Switzerland* **5** *Division of Conservation, Vegetation and Landscape Ecology, University of Vienna, 1030 Vienna, Austria* **6** *ISPRA, Institute for Environmental Protection and Research, and Chair of IUCN SSC Invasive Species Specialist Group, Via V. Brancati 48, 00144, Rome, Italy* **7** *Centre for Ecology & Hydrology, Wallingford, UK, OX10, 8BB* **8** *The Bio-Protection Research Centre, Lincoln University, PO Box 85840, 7648, New Zealand* **9** *Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310, 12587 Berlin, Germany* **10** *Freie Universität Berlin, Department of Biology, Chemistry and Pharmacy, Königin-Luise-Str. 1-3, 14195 Berlin, Germany* **11** *Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Altensteinstr. 34, 14195 Berlin, Germany* **12** *CABI, Rue des Grillons, 2800 Delémont, Switzerland* **13** *Helmholtz Centre for Environmental Research – UFZ, Department of Community Ecology, Theodor-Lieser-Str. 4, 06120 Halle, Germany* **14** *Institute of Biology/Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle, Germany* **15** *German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany* **16** *Environment Agency Austria, Department of Biodiversity and Nature Conservation, Spittelauer Lände 5, 1090 Vienna, Austria* **17** *Institut National de la Recherche Agronomique (INRA), UR633 Zoologie Forestière, 45075- Orléans, France* **18** *Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio s/n, Isla de la Cartuja, 41092 Sevilla, Spain* **19** *Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012-Bern, Switzerland*

Corresponding author: *Jan Pergl* (pergl@ibot.cas.cz)

Academic editor: *L.A. Meyerson* | Received 17 August 2016 | Accepted 29 October 2016 | Published 4 January 2017

Citation: Pergl J, Pyšek P, Bacher S, Essl F, Genovesi P, Harrower CA, Hulme PE, Jeschke JM, Kenis M, Kühn I, Perglová I, Rabitsch W, Roques A, Roy DB, Roy HE, Vilà M, Winter M, Nentwig W (2017) Troubling travellers: are ecologically harmful alien species associated with particular introduction pathways? NeoBiota 32: 1–20. https://doi.org/10.3897/neobiota.32.10199

Copyright *Jan Pergl et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Abstract

Prioritization of introduction pathways is seen as an important component of the management of biological invasions. We address whether established alien plants, mammals, freshwater fish and terrestrial invertebrates with known ecological impacts are associated with particular introduction pathways (release, escape, contaminant, stowaway, corridor and unaided). We used the information from the European alien species database DAISIE (www.europe-aliens.org) supplemented by the EASIN catalogue (European Alien Species Information Network), and expert knowledge.

Plants introduced by the pathways release, corridor and unaided were disproportionately more likely to have ecological impacts than those introduced as contaminants. In contrast, impacts were not associated with particular introduction pathways for invertebrates, mammals or fish. Thus, while for plants management strategies should be targeted towards the appropriate pathways, for animals, management should focus on reducing the total number of taxa introduced, targeting those pathways responsible for high numbers of introductions. However, regardless of taxonomic group, having multiple introduction pathways increases the likelihood of the species having an ecological impact. This may simply reflect that species introduced by multiple pathways have high propagule pressure and so have a high probability of establishment. Clearly, patterns of invasion are determined by many interacting factors and management strategies should reflect this complexity.

Keywords

DAISIE, Europe, fish, ecological impact, introductions, invertebrates, mammals, pathways, plants

Introduction

The management of individual introduction pathways, and corresponding vectors, of alien species is a potentially powerful strategy to prevent new species introductions and thus reduce both the future costs to society as well as negative impacts on biodiversity (Carlton and Ruiz 2005, Hulme 2009, Essl et al. 2015). Pathway management is primarily aimed at eliminating or diminishing the propagule pressure of alien species and reflects the common wisdom that prevention and early action are more cost-effective than managing invaders after they have become established (Leung et al. 2002, Kaiser and Burnett 2010). Information on the pathways of introduction is increasingly incorporated in alien species databases (e.g. IUCN ISSG Global Invasive Species Database, www.issg.org/database, CABI Invasive Species Compendium, www.cabi.org/isc, and European Alien Species Information Network – EASIN, Katsanevakis et al. 2015) and country inventories (e.g. Kühn and Klotz 2003, García-Berthou et al. 2005, Nentwig 2007, Minchin et al. 2013, Roy et al. 2014). This provides an opportunity for comparative assessments of the role of pathways in biological invasions (Wilson et al. 2009, Bacon et al. 2012, 2014) and ultimately developing indicators based on trends in pathways (Rabitsch et al. 2016). This has led to a general framework for classifying pathways of introduction across taxa and environments that includes the identification of regulatory responsibilities (Hulme et al. 2008). A modified version of this general framework has recently been adopted by the UN Convention on Biological Diversity (CBD 2014). Some pathways are increasingly well studied, such as horticulture and forestry as a source for plant invasions (Mack and Erneberg 2002, Dehnen-Schmutz et al. 2007a,

b, Hanspach et al. 2008, Dawson et al. 2009, Pyšek et al. 2009, Essl et al. 2010, Smith et al. 2015, Pergl et al. 2016a, b), ballast water transport and aquaculture disseminating aquatic invaders (Galil et al. 2009, Mizrahi et al. 2015, Nuñes et al. 2015), live plants and plant products introducing pest insects and plant diseases (Roques 2010, Bacon et al. 2012, 2014, Liebhold et al. 2012, Eschen et al. 2015a, b), as well as snails (Bergey et al. 2014) and spiders (Nentwig 2015), the aquarium trade (Maceda-Veiga et al. 2013, Chucholl 2013), tourism (Anderson et al. 2015), the pet trade for terrestrial vertebrate invaders (Duncan et al. 2003, van Wilgen et al. 2010, Garcia-Diaz and Cassey 2014), and – more generally – the online trade (Kikillus et al. 2012, Humair et al. 2015). However, the role of pathways related to unintentional introductions has been difficult to quantify (Lee and Chown 2009, Pyšek et al. 2011, Bacon et al. 2012). Additionally, whether particular introduction pathways are associated disproportionally with the subsequent impacts of alien species has received little attention (Pyšek et al. 2011). Given the increasing rate at which alien species are being introduced around the world and predicted upward trends in the magnitude of major introduction pathways (Hulme 2015a), strategies to manage pathways based on their ultimate ecological risk are a priority. For example, several calls for identifying and managing pathways responsible for the introduction of species with high negative ecological and/or socio-economic impacts have been issued (EU 2014, CBD 2014).

Pathways of introduction and the subsequent impacts caused by invasive alien species (IAS) might be related in three ways (Essl et al. 2015). First, pathways that transport a high richness or abundance of species are more likely to lead to establishment and subsequent impact by a proportion of those species than pathways that carry fewer species or individuals. Second, certain pathways may introduce species into areas of conservation value, e.g. protected or remote areas where impacts may be particularly significant (Hulme 2011, Osyczka et al. 2012, Anderson et al. 2015). Third, some pathways may introduce more damaging species than others, particularly when pathogens are introduced as contaminants of their hosts (Roy et al. 2016). Therefore, identifying those pathways that are associated with impacts would help to prevent the emergence of new high-risk invaders. Yet, pathways and impacts have so far only been analysed together for a few taxonomic groups and particular pathways (e.g. Liebhold et al. 2012) and never across taxonomic groups. Lastly, taxa introduced by multiple pathways and introduced to different regions and habitats have a higher opportunity to become naturalized and then may have a greater probability of causing impact than those arriving on only one pathway (Küster et al. 2008).

Here we address the knowledge gap between impact and introduction pathways by relating for the first time the pathways of introduction of alien species spanning a range of taxonomic groups (plants, mammals, freshwater fish, and terrestrial invertebrates) in Europe to their ecological impacts. The aims of this study are: (i) to explore whether species with known ecological impacts differ in their pathway associations from those species for which no impact has been reported; (ii) to identify for particular alien taxonomic groups which pathways pose the greatest threat; and (iii) to explore whether species transported by multiple pathways are associated with a higher probability of

impact. More generally, the study presents a first attempt to identify the most relevant pathways of introduction of IAS with impact that can provide a data source for governments to fulfil their obligation under the Convention on Biological Diversity, and the recently adopted EU Regulation on IAS (EU 2014).

Methods

Data

Data from DAISIE (2009) database (www.europe-aliens.eu; Pergl et al. 2012) was used as a source of information on impacts of established alien species in Europe. It was also used as a basis for assignment of the pathways of their introduction to Europe for (i) vascular plants, (ii) freshwater fish, and (iii) mammals, while the EASIN catalogue (easin.jrc.ec.europa.eu; Katsanevakis et al. 2015) was used for pathway and impact classification of (iv) terrestrial invertebrates. The classification of introduction pathways follows the scheme of Hulme et al. (2008) that allows their comparison across taxonomic groups as well as between accidental and intentional introductions. Each species was assigned to one or more of the following pathway categories: (i) release (intentional introduction and release into the environment), (ii) escape (intentionally introduced as a commodity, but escaped from culture), (iii) contaminant (unintentional introduction with specified commodity), (iv) stowaway (unintentionally introduced attached to or within a transport vector), (v) corridor (unintentional spread via human transport infrastructures linking previously unconnected regions) or (vi) unaided (unintentional introduction by natural dispersal across political borders following a primary human-mediated introduction in a neighbouring region). The data do not differentiate between the pathways for initial introduction to Europe and those associated with movement among different European countries. Similarly, species are often listed as associated with more than one introduction pathway with no measure of their relative importance. In contrast to other taxonomic groups, the invertebrate data do not allow the exact area of origin to be identified for species that are native in a part of Europe and alien in another part and thus this group included only arrivals from other continents (classified as aliens *to* Europe in DAISIE 2009). Only species confirmed as established in at least one European country (DAISIE regions) were included in the analyses. As information on establishment status is incomplete for some regions of Europe, we also included species for which establishment could not be confirmed but that were found in five or more European regions.

As a second step, species for which introduction pathways had been identified were classified in two groups: those having an ecological impact and those for which no ecological impact had been recorded. For fish, mammals and plants, the information on ecological impacts was retrieved from DAISIE (Vilà et al. 2010). For invertebrates information in DAISIE and EASIN was updated with literature and expert opinion (M. Kenis, W. Rabitsch and A. Roques, unpublished data). Ecological impact was defined as an impact on native species or on the functioning of natural or semi-natural

ecosystems in Europe or in similar climatic and environmental conditions in other continents. There was no assessment of the type of impact or its magnitude.

Statistical analysis

We tested: (i) whether different pathways (release, escape, contaminant, stowaway, corridor and unaided) are associated with higher or lower probability of causing ecological impact and (ii) whether there is a relationship between the likelihood of impacts and the number of pathways through which a species has been introduced. All analyses were based on species counts that were analysed by generalized linear models with a log-link function and Poisson distribution of errors with control for overdispersion (if needed using quasi-Poisson distributions) (Crawley 2007). If the full model including the interaction with taxon was significant, then individual models for particular taxonomic groups were used. To test in which pathways the counts were lower or higher than expected by chance, adjusted standardized residuals of *G*-tests were compared with critical values of a normal distribution (Řehák and Řeháková 1986). The null expectations were thus that the proportion of species with and without ecological impact within an individual pathway is the same across all pathways and that number of species with and without impact are not related to number of pathways. The test for multiple pathways was done by summing up the number of pathways per species. All analyses were performed in R 3.0.2 (R Core Team 2015).

Results

Differences in pathway frequencies by taxonomic groups

There were 2529 vascular plant, 75 mammal, 107 fish and 1314 terrestrial invertebrate taxa (species or subspecies) with at least one pathway category assigned. The coverage of identified pathways for the taxa ranged from 98% for fish to 59% in plants (Table 1). The most frequently represented pathways differed between taxa. In plants, the most frequent pathway was escape, recorded for 58% of the total species number. Mammals had a high proportion of release and escape (49% and 41%, respectively). Among freshwater fishes, there were 43% escaped and 36% released species. In contrast, 76% of the terrestrial invertebrates were introduced as contaminants of commodities (Table 1).

Impact associated with pathways in different taxonomic groups

Among the established taxa with known introduction pathway, there were 250 vascular plants (6.2% of the total), 38 mammals (61.3%), 52 fishes (48.6%) and 80 terrestrial

Table 1. Percentages and observed counts (in brackets) of pathways identified for individual taxonomic groups. Totals show the percentage and number of alien species for which a pathway is known. Note that species can be associated with more than one pathway, so the counts do not add up to total. 'No pathway data' shows the percentage from all assessed taxa (total + no data) and the number of species that meet the criteria of establishment or widespread distribution in Europe, but for which there is no precise enough information on pathways.

	Release	Escape	Contaminant	Stowaway	Corridor	Unaided	Total	No pathway data
Plants	18.4 (638)	58.3 (2016)	19.4 (670)	2.7 (92)	0 (1)	1.2 (42)	59.4 (2529)	40.6 (1732)
Mammals	48.8 (40)	41.5 (34)	0 (0)	0 (0)	0 (0)	9.8 (8)	72.0 (54)	28.0 (21)
Fish	35.6 (74)	42.8 (89)	0 (0)	1.4 (3)	6.7 (14)	13.5 (28)	98.1 (105)	1.9 (2)
Terrestrial invertebrates	11.7 (156)	2.5 (34)	76.3 (1020)	9.0 (120)	0.4 (6)	0.0 (0)	75.0 (1314)	25.0 (438)

invertebrates (6.1%) with documented or strongly supposed ecological impact (Table 2). There was a significantly higher frequency of taxa with impact within mammals and fishes than in plants and invertebrates (two-way interaction taxon × impact χ^2 = 208.71; df = 3; P < 0.001). Overall, the frequency of ecological impacts differed significantly among pathways and taxa (three-way interaction taxon × pathway × impact: χ^2 = 29.11; df = 15; P = 0.015). Within the particular taxonomic group, the impacts were significantly different among pathways for plants (χ^2 = 32.54; df = 5; P < 0.001) but not so for invertebrates, mammals or fish. As discussed below, the results might be masked by lower statistical power of the test in these taxon groups due to high numbers of pathways with zeros and that mammals and fish are generally species-poor groups. For plants exerting ecological impact, the significant difference among pathways was mainly due to disproportionately more counts than expected for release, corridor and unaided pathways, and disproportionately fewer for contaminants (Table 2).

The role of multiple pathways

The maximum number of pathways recorded for species with ecological impact was four, represented by five plants (e.g. *Elodea canadensis* – Canadian waterweed, *Galinsoga parviflora* – gallant soldier, and *Senecio vernalis* – Eastern groundsel) and two fish (*Oncorhynchus gorbuscha* – pink salmon, and *O. mykiss* – rainbow trout). For mammals, the maximum number of pathways was three, recorded in six species (e.g. *Cervus nippon* – sika deer, *Ondatra zibethicus* – muskrat, *Procyon lotor* – raccoon). For terrestrial invertebrates with impact, the maximum number of pathways was two (*Lasius neglectus* – garden ant, and *Linepithema humile* – Argentine ant) (Fig. 1).

The taxonomic groups did not differ in their impact related to the number of pathways (three-way interaction taxon × number of pathways × impact: χ^2 = 8.01; df = 9; p=0.53), but pooled across taxa, having multiple pathways increased the probability of recording impact (χ^2 = 170.11; df = 3; P < 0.001). Taxa associated with only one

Table 2. Percentages and observed counts (in brackets) for ecological impact across pathways among taxonomic groups. Note that species can be associated with more than one pathway. Higher and lower values than expected by chance (based on *G*-tests) are indicated by asterisks (*<0.05, ** < 0.01, *** < 0.001) and corresponding sign (↓ observed counts lower than expected, ↑observed counts higher than expected). Significant effects of pathways are highlighted.

Ecological Impact	Taxa with impact	Release		Escape		Contaminant		Stowaway		Corridor		Unaided	
		No	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes
Plants	6.2 (250)	15.5 (537)	↑2.9 (101)**	52 (1800)	6.2 (216)	17.7 (613)	↓1.6 (57)*	0 (0)	0 (1)	2.1 (74)	↑0.5 (18)*	0.9 (32)	↑0.3 (10)*
Mammals	61.3 (38)	14.6 (12)	34.1 (28)	7.3 (6)	34.1 (28)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.2 (1)	8.5 (7)
Fish	48.6 (52)	16.8 (35)	18.8 (39)	20.2 (42)	22.6 (47)	0 (0)	0 (0)	3.8 (8)	2.9 (6)	1.0 (2)	0.5 (1)	4.8 (10)	8.7 (18)
Terrestrial invertebrates	6.1 (80)	11.6 (152)	0.3 (4)	2.6 (34)	0.0 (0)	73.1 (961)	4.5 (59)	8.4 (111)	0.7 (9)	0.3 (4)	0.2 (2)	0.0 (0)	0.0 (0)

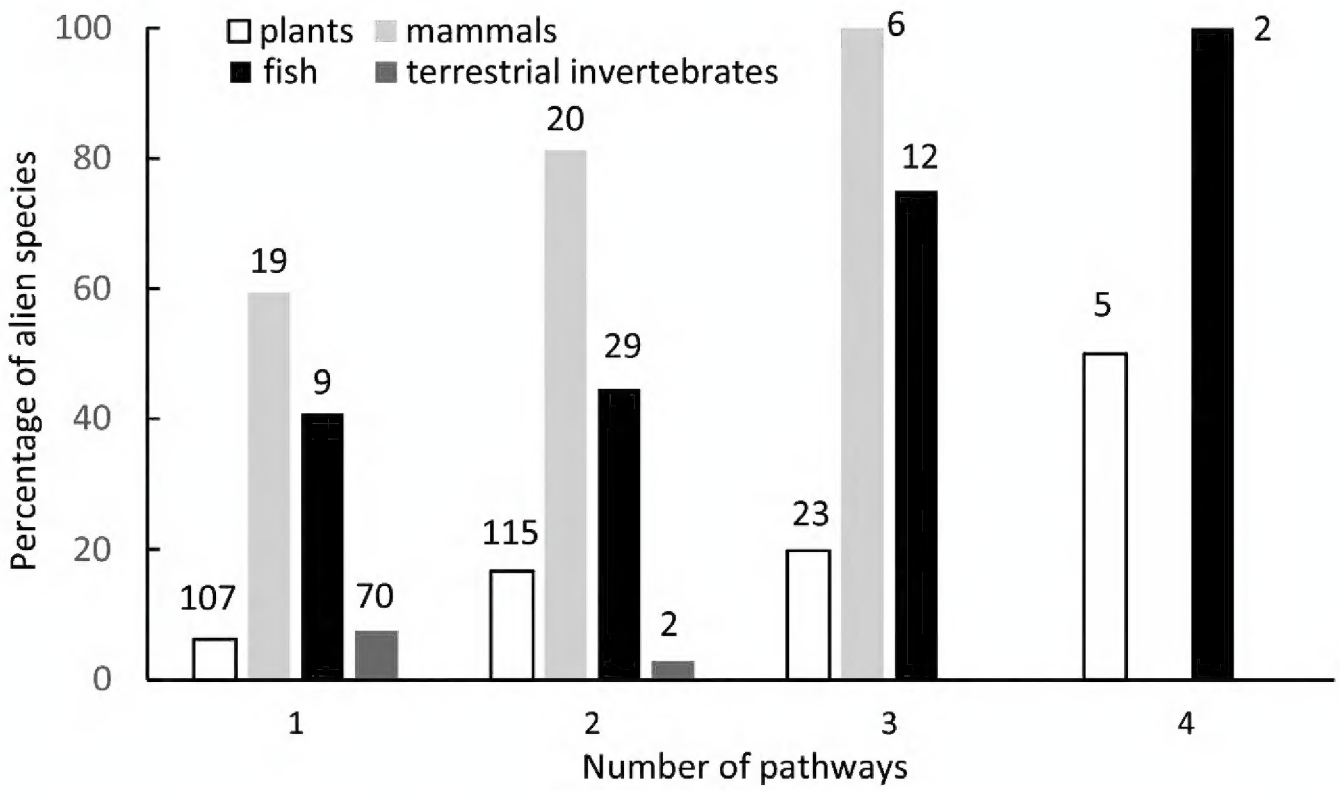

Figure 1. Percentage of alien species with impact in relation to the number of introduction pathways. The height of the bar indicates the percentage of the number of taxa with impact within the taxonomic group of species that are introduced via the given number of pathways. Numbers above bars indicate the numbers of species with impact for each taxonomic group and for the given number of pathways.

pathway were less likely to have an impact than expected by chance (G = 3.47, P < 0.001), while those associated with two and three pathways were more likely (G = 4.45, P < 0.001; G = 2.62, P < 0.01). The number of taxa without impact and introduced by four pathways was lower than expected by chance (G = 2.89, P < 0.01). Combinations of pathways per taxonomic group are shown in Appendix 1.

Discussion

Differences among taxonomic groups

The relationship between impacts and pathways differed with respect to taxonomic groups, but for most taxa no major significant differences among pathways were found. For plants, pathways vary in the proportion of species with impact they deliver, while for invertebrates, fish and mammals this was not the case. For example, among escaped mammals, in a group featuring prominent examples of escaped fur animals with high ecological impacts (*Neovison vison* – American mink, *Ondatra zibethicus* – muskrat), there were no significant differences between numbers of species with and without impacts. Further, the number of species with impact arriving by a given pathway is also important. For example, the absolute number of escaped plants with impact was twice as high as that of released plants with impact, despite the difference between the two pathways not being statistically significant. Similarly, fewer than expected species

of plants causing impact are introduced as contaminants, but absolute values for terrestrial invertebrates indicate a high importance of this pathway compared to release.

That pathways do not significantly affect the probability of impact of vertebrates may be related to the generally high invasion success of this group (Jeschke and Strayer 2005, Jeschke 2008), as well as to a high percentage of species with impacts compared to plants and invertebrates (Table 2). If vertebrates are introduced and establish there is a high probability of them having impact regardless of the pathway on which they arrive. Furthermore, identifying pathways causing negative environmental impacts by alien vertebrates may require more detailed analyses than for other taxonomic groups. For example, to assess the role of the pet trade, which is a subset of the escape category, it would be important to carry out analyses at a finer level than is currently the case. Considering intentional (release, escape) *vs* unintentional pathways (contaminant, stowaway, corridor and unaided) across all taxa, our results indicate that the latter are associated with impact less frequently than expected, and *vice versa*. In absolute numbers, unintentional pathways were more common for invertebrates, but not so for plants. However, the pattern is blurred by the fact that many species were introduced through several pathways, including both intentional and unintentional. For example, for plants, Pyšek et al. (2011) found that unintentionally introduced species invaded a wider range of semi-natural habitats than intentionally introduced species; hence the risk arising from unintentional introductions should not be underestimated.

An important question is whether species introduced by multiple pathways have an advantage because of a higher propagule pressure or an increased probability to reach a more diverse range of suitable sites. Unfortunately, robust data for propagule pressure that can be compared across individual pathways for the respective taxonomic groups are rarely available. If such data exist, they are limited to specific pathways such as direct release for biocontrol (Rossinelli and Bacher 2015) or landscaping (but see Lee and Chown 2009). Our knowledge thus mostly depends on proxies such as trade volume, numbers of botanic gardens, human population density or road density (Carlton and Ruiz 2005, Wilson et al. 2009, Kaluza et al. 2010, Pyšek et al. 2010; Hulme 2015b). Although some taxonomic groups such as invertebrates are highly dependent on one specific pathway, in general, the number of introduction pathways can be used as another proxy for propagule pressure. It appears that ecological impacts are more likely to occur if plants are introduced by multiple pathways. Besides profiting from increased propagule pressure, it is also possible that species introduced by multiple pathways have a greater chance of being introduced to a wider range of habitats or are also ecologically more versatile than those arriving on single pathways. In plants, the existence of multiple pathways usually includes escape from cultivation, reflecting the dominant role of horticultural introductions, which is for many species combined with introduction as contaminants. The combination of pathways that favours high impact fishes is release and escape, but these two pathways are also often accompanied with unintentional introductions. It seems that at least in these two taxonomic groups, the predisposition for opportunistic dispersal may be determined by the same traits as

the ability to escape from capture or cultivation. Still, there are fishes with severe impacts introduced by a single pathway, e.g. *Leuciscus leuciscus* (common dace), *Clarias gariepinus* (African sharptooth catfish), *Oreochromis niloticus* (Nile tilapia), *or Polyodon spathula* (American paddlefish). For terrestrial invertebrates, species with impact introduced as contaminants dominate, which highlights the importance of this pathway and the fact that this pathway is responsible for high propagule pressure. However, it is likely that a large number of these species are also introduced as stowaways but this pathway is hugely underestimated because it is so difficult to assess (A. Roques, unpublished data).

Relating impact to pathways: what data are available?

Although a simple yes/no classification of ecological impact provides basic information, it is evident that impacts manifest over a wide range of magnitudes, from local population declines to global extinctions, or from minor perturbations to massively adverse ecological and economic cascades. A yes/no impact classification lumps together species with low ecological impact, e.g. *Mahonia aquifolium* (Oregon-grape), with high-impact species such as *Fallopia* spp. (knotweeds) (Kumschick et al. 2015a). Similarly, while there are over 600 alien terrestrial invertebrate species (mostly insects) classified as having an ecological impact in DAISIE, an extensive literature survey of ecological impacts attributed to invasive insects found published records for less than 10 species in Europe (Kenis et al. 2009). On the other hand, using other impact criteria, Vaes-Petignat and Nentwig (2014) described impacts for 64 of the 77 most widely spread terrestrial arthropods alien to Europe. However, despite recent attempts to classify impacts more precisely (Nentwig et al. 2010, 2016, Kumschick and Nentwig 2011, Kenis et al. 2012, Blackburn et al. 2014, Jeschke et al. 2014, Kumschick et al. 2015b, Rumlerová et al. 2016), such information is rarely available for a large number of species. Low sample size is a constraint for the statistical analysis, particularly for alien mammals and fishes, and limits the power of finding relevant patterns despite the severe impacts that these two taxonomic groups are known to have on biodiversity (Kumschick et al. 2015a). Differences in the quality of impact data (Hulme et al. 2013) among taxonomic groups are not only due to species numbers or recorded impacts, but also result from the research activity (e.g. ease of study or attractiveness). The frequent impacts of released species may be due to the fact that some of those species are introduced for a purpose that requires having an ecological impact (e.g. plant species for dune stabilization, invertebrates for biocontrol) and are better scrutinized for any potential adverse (and unintended) impacts on native species. About 110 released invertebrates (mostly biocontrol agents) have been classified as having an ecological impact in Europe (DAISIE 2009). Only three are known to have some measurable negative impact on native species, the parasitoids *Cales noaki* and *Lysiphlebus testaceipes* (Kenis et al. 2009), and the harlequin ladybird *Harmonia axyridis* (Roy et al. 2012, 2016).

Management recommendations

The management of IAS with negative impacts on the environment and on human well-being is subject to efforts at national, continental and global levels (CBD 2014, Aichi Biodiversity Target 9). The categories used for the present analysis are consistent with the standard categorization of pathways of introduction of IAS presented by the CBD and recommended for identifying and prioritizing pathways (CBD 2014). At the European scale, the new EU Regulation on IAS, entered into force on 1 January 2015 (EU 2014, Genovesi et al. 2015), calls EU Member States to identify the pathways of unintentional introduction and spread of IAS of Union concern, and to effectively manage them through specific action plans.

The CBD and EU legislation confirm that policies are focusing on the prioritization of pathways in order to prevent the introduction of IAS (Meyerson and Reaser 2003, Hulme 2009, 2011). This covers managing or preventing the introduction of new species to a particular region and mitigating their impacts by regulation of intentional and unintentional introductions (Wittenberg and Cock 2001, Caffrey et al. 2014). To make pathway management work efficiently, it needs to be built on rigorous data on impacts of alien species, and how these interact with individual pathways. Some pathways and taxonomic groups, plants and invertebrates particularly, contribute disproportionally more to the overall risk from alien species with documented impacts, and these should receive increased attention. However, to fully assess the potential of each particular pathway, not only is it necessary to consider the proportion of species with negative impacts, but also the absolute number of species introduced along each pathway.

Using proportions as a measure emphasizes the release pathway as posing greater risk, regardless of the taxonomic group, while using absolute species numbers prioritizes the escape and contaminant pathways. The other pathways associated with arrival of IAS can be assumed to be less important for management and monitoring. Legislation, early warning systems and rapid response mechanisms should be primarily targeted at intentional introductions (release and escape) and species introduced unintentionally as contaminants (for which the pathway of arrival can be identified). An accurate identification of the pathways of introduction and spread of alien species is essential for efficient management of invasions, and in this regard it is important to adopt a standard terminology and categorization, as recommended by the CBD (Hulme et al. 2016); a standardized approach will be essential in enforcing the EU Legislation, to ensure that action by EU member states is coordinated. Also, the present study highlights that the proportions of alien species with negative ecological impacts are taxon-specific, a finding that should be reflected by legislation and pathway management. However, in many cases at the present level of understanding, the best predictor of the relevance of an introduction pathway is the total number of species that are associated with it. Furthermore, we showed that the results of this study are highly dependent on the availability of data and it is necessary to better reflect the scales of impacts ranging from minimal to massive to improve understanding and management of IAS.

Therefore, we encourage further work on the approach outlined here through more detailed analyses of individual pathways, their association with IAS, consideration of spatial and temporal variation in pathway trends (Padilla and Williams 2004, Copp et al. 2010, Maceda-Veiga et al. 2013, Hulme 2015b), inclusion of more detailed descriptions of the magnitude and/or types of impact (Nentwig et al. 2010, 2016, Blackburn et al. 2014, Kumschick et al. 2015a) and consideration of other taxa that were not included in the present study such as fungi, and considering interactions and synergies between pathways (Roy et al. 2016). As for most taxa it was not possible to detect major differences in the way in which IAS arrive and so until robust and comprehensive information on impact is available, we should not focus on subtle differences between the pathways of arrival for different taxonomic groups, but instead consider the most common pathways for all taxa and pathways that are most easily managed. Thus pathways that deliver many species should become a management priority.

Author contributions

J.P., P.P. and W.N conceived the ideas, AR, MK and WR revised data on impacts of insects and all authors contributed to writing the paper.

Acknowledgements

Contributions from Vojtěch Jarošík and Francesca Gherardi who both passed away during the work on the project are acknowledged with deep sadness. The study was supported by projects SCIEX, DAISIE and COST TD1209 (Alien Challenge). JP, PP and IP were funded by long-term research development project RVO 67985939 (The Czech Academy of Sciences), and projects no. 14-36079G (Centre of Excellence PLADIAS) and P504/11/1028 from the Czech Science Foundation. PP acknowledges support from Praemium Academiae award from The Czech Academy of Sciences. JMJ acknowledges support from the ERA-Net BiodivERsA (project FFII), with the national funder German Research Foundation DFG (JE 288/7-1), and through the DFG grant JE 288/9-1. MV has been funded through the Severo Ochoa Program for Centres of Excellence in R+D+I (SEV-2012-0262) and IMPLANTIN (CGL2015-65346-R).

References

Anderson LG, Rocliffe S, Haddaway NR, Dunn AM (2015) The role of tourism and recreation in the spread of non-native species: a systematic review and meta-analysis. PLoS ONE 10: e0140833. doi: 10.1371/journal.pone.0140833

Bacon SJ, Aebi A, Calanca P, Bacher S (2014) Quarantine arthropod invasions in Europe: the role of climate, hosts and propagule pressure. Diversity and Distributions 20: 84–94. doi: 10.1111/ddi.12149

Bacon SJ, Bacher S, Aebi A (2012) Gaps in border controls are related to quarantine alien insect invasions in Europe. PLoS ONE 7: e47689. doi: 10.1371/journal.pone.0047689

Bergey EA, Figueroa LL, Mather CM, Martin RJ, Ray EJ, Kurien JT, Westrop DR, Suriyawong P (2014) Trading in snails: plant nurseries as transport hubs for non-native species. Biological Invasions 16: 1141–1451. doi: 10.1007/s10530-013-0581-1

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P, Bacher S (2014) A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biology 12: e1001850. doi: 10.1371/journal.pbio.1001850

Caffrey JM et al. (2014) Tackling invasive alien species in Europe: the top 20 issues. Management of Biological Invasions 5: 1–20. doi: 10.3391/mbi.2014.5.1.01

Carlton JT, Ruiz GM (2005) Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK (Eds) Invasive alien species. Island Press, Washington, DC, 36–58.

CBD (2014) Pathways of introduction of invasive species, their prioritization and management; UNEP/CBD/SBSTTA/18/9/Add.1. https://www.cbd.int/doc/meetings/sbstta/sbstta-18/official/sbstta-18-09-add1-en.pdf

CBD (2011) The Strategic Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets, COP CBD Tenth Meeting UNEP/CBD/COP/DEC/X/2. http://www.cbd.int/sp/targets/rationale/target-9

Chucholl C (2013) Invaders for sale: trade and determinants of introduction of ornamental freshwater crayfish. Biological Invasions 15: 125–141. doi: 10.1007/s10530-012-0273-2

Copp GH, Vilizzi L, Gozlan RE (2010) The demography of introduction pathways, propagule pressure and occurrences of non-native freshwater fish in England. Aquatic Conservation: Marine and Freshwater Ecosystems 20: 595–601. doi: 10.1002/aqc.1129

Crawley MJ (2007) The R book. John Wiley & Sons, Chichester. doi: 10.1002/9780470515075

DAISIE (Eds) (2009) Handbook of alien species in Europe. Springer, Berlin.

Dawson W, Burslem DFRP, Hulme PE (2009) Factors explaining alien plant invasion success in a tropical ecosystem differ at each stage of invasion. Journal of Ecology 97: 657–665. doi: 10.1111/j.1365-2745.2009.01519.x

Dehnen-Schmutz K, Touza J, Perrings C, Williamson M (2007a) The horticultural trade and ornamental plant invasions in Britain. Conservation Biology 21: 224–231. doi: 10.1111/j.1523-1739.2006.00538.x

Dehnen-Schmutz K, Touza J, Perrings C, Williamson M (2007b) A century of the ornamenta plant trade and its impact on invasion success. Diversity and Distributions 13: 527–534. doi: 10.1111/j.1472-4642.2007.00359.x

Duncan RP, Blackburn TM, Sol D (2003) The ecology of bird introductions. Annual Review of Ecology, Evolution, and Systematics 34: 71–98. doi: 10.1146/annurev.ecolsys.34.011802.132353

Eschen R, Grégoire J-C, Hengeveld GM, de Hoop BM, Rigaux L, Potting RPJ (2015a) Trade patterns of the tree nursery industry in Europe and changes following findings of citrus longhorn beetle, *Anoplophora chinensis* Forster. NeoBiota 26: 1–20. doi: 10.3897/neobiota.26.8947

Eschen R, Roques A, Santini A (2015b) Taxonomic dissimilarity in patterns of interception and establishment of alien arthropods, nematodes and pathogens affecting woody plants in Europe. Diversity and Distributions 21: 36–45. doi: 10.1111/ddi.12267

Essl F, Bacher S, Blackburn TM, Booy O, Brundu G, Brunel S, Cardoso A-C, Eschen R, Gallardo B, Galil B, García-Berthou E, Genovesi P, Groom Q, Harrower C, Hulme PE, Katsanevakis S, Kenis M, Kühn I, Kumschick S, Martinou AF, Nentwig W, O'Flynn C, Pagad S, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Roques A, Roy HE, Scalera R, Schindler S, Seebens H, Vanderhoeven S, Vilà M, Wilson JRU, Zenetos A, Jeschke JM (2015) Crossing frontiers in tackling pathways of biological invasions. BioScience 65: 769–782. doi: 10.1093/biosci/biv082

Essl F, Dietmar M, Dullinger S, Mang T, Hulme PE (2010) Selection for commercial forestry determines global patterns of alien conifer invasions. Diversity and Distributions 16: 911–921. doi: 10.1111/j.1472-4642.2010.00705.x

EU (2014) Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species.

Galil BS, Gollasch S, Minchin D, Olenin S (2009) Alien marine biota of Europe. In: DAISIE, Handbook of alien species in Europe. Springer, Berlin, 93–104. doi: 10.1007/978-1-4020-8280-1_7

García-Berthou E, Alcaraz C, Pou-Rovira Q, Zamora L, Coenders G, Feo C (2005) Introduction pathways and establishment rates of invasive aquatic species in Europe. Canadian Journal of Fisheries and Aquatic Sciences 62: 453–463. doi: 10.1139/f05-017

García-Díaz P, Cassey P (2014) Patterns of transport and introduction of exotic amphibians in Australia. Diversity and Distributions 20: 455–466. doi: 10.1111/ddi.12176

Genovesi P, Carboneras C, Vilà M, Walton P (2015) EU adopts innovative legislation on invasive species: a step towards a global response to biological invasions? Biological Invasions 17: 1307–1311. doi: 10.1007/s10530-014-0817-8

Hanspach J, Kühn I, Pyšek P, Boos E, Klotz S (2008) Correlates of naturalization and occupancy of introduced ornamentals in Germany. Perspectives in Plant Ecology, Evolution and Systematics 10: 241–250. doi: 10.1016/j.ppees.2008.05.001

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46: 10–18. doi: 10.1111/j.1365-2664.2008.01600.x

Hulme PE (2011) Addressing the threat to biodiversity from botanic gardens. Trends in Ecology and Evolution 26: 168–74. doi: 10.1016/j.tree.2011.01.005

Hulme PE (2015a) Invasion pathways at a crossroad: policy and research challenges for managing alien species introductions. Journal of Applied Ecology 52: 1418–1424. doi: 10.1111/1365-2664.12470

Hulme PE (2015b) Resolving whether botanic gardens are on the road to conservation or a pathway for plant invasions. Conservation Biology 29: 816–824. doi: 10.1111/cobi.12426

Hulme PE, Bacher S, Kenis M, Klotz S, Kuhn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. Journal of Applied Ecology 45: 403–414. doi: 10.1111/j.1365-2664.2007.01442.x

Hulme PE, Bacher S, Kenis M, Kühn I, Pergl J, Pyšek P, Roques A, Vilà M (2016) Blurring alien introduction pathways risks losing the focus on invasive species policy. Conservation Letters. doi: 10.1111/conl.12262

Hulme PE, Pyšek P, Jarošík V, Pergl J, Schaffner U, Vilà M (2013) Bias and error in current knowledge of plant invasions impacts. Trends in Ecology and Evolution 28: 212–218. doi: 10.1016/j.tree.2012.10.010

Humair F, Humair L, Kuhn F, Kueffer Ch (2015) E-commerce trade in invasive plants. Conservation Biology 29: 1658–1665. doi: 10.1111/cobi.12579

Jeschke JM (2008) Across islands and continents, mammals are more successful invaders than birds. Diversity and Distributions 14: 913–916. doi: 10.1111/j.1472-4642.2008.00488.x

Jeschke JM, Bacher S, Blackburn TM, Dick JTA, Essl F, Evans T, Gaertner M, Hulme PE, Kühn I, Mrugała A, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Winter M, Kumschick S (2014) Defining the impact of non-native species. Conservation Biology 28: 1188–1194. doi: 10.1111/cobi.12299

Jeschke JM, Strayer DL (2005) Invasion success of vertebrates in Europe and North America. Proceedings of the National Academy of Sciences of the United States of America 102: 7198–7202. doi: 10.1073/pnas.0501271102

Kaiser BA, Burnett KM (2010) Spatial economic analysis of early detection and rapid response strategies for an invasive species. Resource and Energy Economics 32: 566–585. doi: 10.1016/j.reseneeco.2010.04.007

Kaluza P, Kölzsch A, Gastner MT, Blasius B (2010) The complex network of global cargo ship movements. Journal of the Royal Society Interface 7: 1093–1103. doi: 10.1098/rsif.2009.0495

Katsanevakis S, Deriu I, D'Amico F, Nuñes AL, Pelaez Sanchez S, Crocetta F, Arianoutsou M, Bazos I, Christopoulou A, Curto G, Delipetrou P, Kokkoris Y, Panov VE, Rabitsch W, Roques A, Scalera R, Shirley SM, Tricarico E, Vannini A, Zenetos A, Zervou S, Zikos A, Cardoso AC (2015) European Alien Species Information Network (EASIN): supporting European policies and scientific research. Management of Biological Invasions 6: 147–157. doi: 10.3391/mbi.2015.6.2.05

Kenis M, Auger-Rozenberg MA, Roques A, Timms L, Péré C, Cock MJW, Settele J, Augustin S, Lopez-Vaamonde C (2009) Ecological effects of invasive alien insects. Biological Invasions 11: 21–45. doi: 10.1007/s10530-008-9318-y

Kenis M, Bacher S, Baker RHA, Branquart E, Brunel S, Holt J, Hulme PE, MacLeod A, Pergl J, Petter F, Pyšek P, Schrader G, Sissons A, Starfinger U, Schaffner U (2012) New protocols to assess the environmental impact of pests in the EPPO decision support scheme for pest risk analysis. Bulletin OEPP/EPPO Bulletin 46: 21–27. doi: 10.1111/epp.2527

Kikillus KH, Hare KM, Hartley S (2012) Online trading tools as a method of estimating propagule pressure via the pet-release pathway. Biological Invasions 14: 2657–2664. doi: 10.1007/s10530-012-0262-5

Kühn I, Klotz S (2003) The alien flora of Germany - basics from a new German database. In: Child LE, Brock JH, Brundu G, Prach K, Pyšek P, Wade PM, Williamson M (Eds) Plant invasions: ecological threats and management solutions. Backhuys, Leiden, 89–100.

Küster EC, Kühn I, Bruelheide H, Klotz S (2008) Trait interactions help explain plant invasion success in the German flora. Journal of Ecology 96: 860–868. doi: 10.1111/j.1365-2745.2008.01406.x

Kumschick S, Bacher S, Evans T, Marková Z, Pergl J, Pyšek P, Vaes-Petignat S, van der Veer G, Vilà M, Nentwig W (2015a) Comparing impacts of alien plants and animals using a standard scoring system. Journal of Applied Ecology 52: 552–561. doi: 10.1111/1365-2664.12427

Kumschick S, Gaertner M, Vilà M, Essl F, Jeschke JM, Pyšek P, Ricciardi A, Bacher S, Blackburn TM, Dick JTA, Evans T, Hulme PE, Kühn I, Mrugała A, Pergl J, Rabitsch W, Richardson DM, Sendek A, Winter M (2015b) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. BioScience 65: 55–63. doi: 10.1093/biosci/biu193

Kumschick S, Nentwig W (2011) Some alien birds have as severe an impact as the most effectual alien mammals in Europe. Biological Conservation 143: 2757–2762. doi: 10.1016/j.biocon.2010.07.023

Lee JE, Chown SL (2009) Breaching the dispersal barrier to invasion: quantification and management. Ecological Applications 19: 1944–1959. doi: 10.1890/08-2157.1

Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis M, Lamberti G (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London B 269: 2407–2413. doi: 10.1098/rspb.2002.2179

Liebhold A, Brockerhoff E, Garrett L, Parke J, Britton K (2012) Live plant imports: the major pathway for the forest insect and pathogen invasions of the US. Frontiers in Ecology and the Environment 10: 135–143. doi: 10.1890/110198

Maceda-Veiga A, Escribano-Alacid J, de Sostoa A, García-Berthou E (2013) The aquarium trade as a potential source of fish introductions in southwestern Europe. Biological Invasions 15: 2707–2716. doi: 10.1007/s10530-013-0485-0

Mack R, Erneberg M (2002) The United States naturalized flora: largely the product of deliberate introductions. Annals of the Missouri Botanical Garden 89: 176–189. doi: 10.2307/3298562

Meyerson LA, Reaser JK (2003) Bioinvasions, bioterrorism, and biosecurity. Frontiers in Ecology and the Environment 1: 307–314. doi: 10.2307/3868091

Minchin D, Cook EJ, Clark PF (2013) Alien species in British brackish and marine waters. Aquatic Invasions 8: 3–19. doi: 10.3391/ai.2013.8.1.02

Mizrahi G, Shemesh E, van Ofwegen L, Tchernov D (2015) First record of *Aequorea macrodactyla* (Cnidaria, Hydrozoa) from the Israeli coast of the eastern Mediterranean Sea, an alien species indicating invasive pathways. NeoBiota 26: 55–70. doi: 10.3897/neobiota.26.8278

Nentwig W (2007) Pathways in animal invasions. In: Nentwig W (Ed.) Biological invasions. Springer, Berlin Heidelberg, 11–27. doi: 10.1007/978-3-540-36920-2_2

Nentwig W (2015) Introduction, establishment rate, pathways and impact of spiders alien to Europe. Biological Invasions 17: 2757–2778. doi: 10.1007/s10530-015-0912-5

Nentwig W, Bacher S, Pyšek P, Vilà M, Kumschick S (2016) The generic impact scoring system (GISS): a standardized tool to quantify the impacts of alien species. Environmental Monitoring and Assessment 188: 315. doi: 10.1007/s10661-016-5321-4

Nentwig W, Kühnel E, Bacher S (2010) A generic impact-scoring system applied to alien mammals in Europe. Conservation Biology 24: 302–311. doi: 10.1111/j.1523-1739.2009.01289.x

Nuñes AL, Tricarico E, Panov VE, Cardoso AC, Katsanevakis S (2015) Pathways and gateways of freshwater invasions in Europe. Aquatic Invasions 10: 359–370. doi: 10.3391/ai.2015.10.4.01

Osyczka P, Mleczko P, Karasiński D, Chlebicki A (2012) Timber transported to Antarctica: a potential and undesirable carrier for alien fungi and insects. Biological Invasions 14: 15–20. doi: 10.1007/s10530-011-9991-0

Padilla DK, Williams SL (2004) Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. Frontiers in Ecology and the Environment 2: 131–138. doi: 10.1890/1540-9295(2004)002[0131:BBWAAO]2.0.CO;2

Pergl J, Nentwig W, Winter M, Bacher S, Essl F, Genovesi P, Hulme PE, Jarošík V, Kühn I, Pyšek P, Roques A, Roy D, Vilà M, Roy H (2012) Progress on DAISIE: alien species inventories in Europe updated. In: Neobiota 2012, 7th European Conference on Biological Invasions, Pontevedra, Spain, 12–14 Sept 2012.

Pergl J, Sádlo J, Petřík P, Danihelka J, Chrtek J Jr, Hejda M, Moravcová L, Perglová I, Štajerová K, Pyšek P (2016a) Dark side of the fence: ornamental plants as a source of wild-growing flora in the Czech Republic. Preslia 88: 163–184.

Pergl J, Sádlo J, Petrusek A, Laštůvka Z, Musil J, Perglová I, Šanda R, Šefrová H, Šíma J, Vohralík V, Pyšek P (2016b) Black, Grey and Watch Lists of alien species in the Czech Republic based on environmental impacts and management strategy. NeoBiota 28: 1–37. doi: 10.3897/neobiota.28.4824

Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon PW, Desprez-Loustau A-M, Nentwig W, Pergl J, Poboljšaj K, Rabitsch W, Roques A, Roy DB, Shirley S, Solarz W, Vilà M, Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. Proceedings of the National Academy of Sciences of the United States of America 107: 12157–12162. doi: 10.1073/pnas.1002314107

Pyšek P, Jarošík V, Pergl J (2011) Alien plants introduced by different pathways differ in invasion success: unintentional introductions as greater threat to natural areas? PLoS ONE 6: e24890. doi: 10.1371/journal.pone.0024890

Pyšek P, Křivánek M, Jarošík V (2009) Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecology 90: 2734–2744. doi: 10.1890/08-0857.1

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rabitsch W, Genovesi P, Scalera R, Biała K, Josefsson M, Essl F (2016) Developing and testing alien species indicators for Europe. Journal for Nature Conservation 29: 89–96. doi: 10.1016/j.jnc.2015.12.001

Řehák J, Řeháková B (1986) Analýza kategorizovaných dat v sociologii [Analysis of categorical data in sociology]. Academia, Praha.

Roques A (2010) Alien forest insects in a warmer world and a globalized economy: impacts of changes in trade, tourism and climate on forest biosecurity. New Zealand Journal of Forestry Science 40: S77–S94.

Rossinelli S, Bacher S (2015) Higher establishment success in specialized parasitoids: support for the existence of trade-offs in the evolution of specialization. Functional Ecology 29: 277–284. doi: 10.1111/1365-2435.12323

Roy HE, Adriaens T, Isaac NJB, Kenis M, Onkelinx T, San Martin G, Brown PMJ, Hautier L, Poland R, Roy DB, Comont R, Eschen R, Frost R, Zindel R, Van Vlaenderen J, Nedvěd O, Ravn HP, Grégoire J-C, de Biseau J-C, Maes D (2012) Invasive alien predator causes rapid declines of native European ladybirds. Diversity and Distribution 18: 717–725. doi: 10.1111/j.1472-4642.2012.00883.x

Roy HE, Brown PMJ, Adriaens T et al. (2016) The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and ecology. Biological Invasions 18: 997–1044. doi: 10.1007/s10530-016-1077-6

Roy HE, Hesketh H, Purse BV, Eilenberg J, Santini A, Scalera R, Stentiford GD, Adriaens T, Bacela-Spychalska K, Bass D, Beckmann K, Bessell P, Bojko J, Booy O, Cardoso AC, Essl F, Groom Q, Harrower C, Kleespies R, Martinou AF, van Oers MM, Peeler EJ, Pergl J, Rabitsch W, Roques A, Schaffner F, Schindler S, Schmidt BR, Schonrogge K, Smith J, Solarz W, Stewart A, Stroo A, Tricarico E, Vannini A, Vilà M, Woodward S, Wynns AA, Dunn AM (2016) Alien pathogens on the Horizon: opportunities for predicting their threat to wildlife. Conservation Letters (in press). doi: 10.1111/conl.12297

Roy HE, Preston CD, Harrower CA, Rorke SL, Noble D, Sewell J, Walker K, Marchant J, Seeley B, Bishop J, Jukes A, Musgrove A, Pearman D (2014) GB Non-native Species Information Portal: documenting the arrival of non-native species in Britain. Biological Invasions 16: 2495–2505. doi: 10.1007/s10530-014-0687-0

Rumlerová Z, Vilà M, Pergl J, Nentwig W, Pyšek P (2016) Scoring environmental and socio-economic impacts of alien plants invasive in Europe. Biological Invasions 18(12): 3697–3711. doi: 10.1007/s10530-016-1259-2

Smith LL, Allen DJ, Barney J (2015) The thin green line: sustainable bioenergy feedstocks or invaders in waiting. NeoBiota 25: 47–71. doi: 10.3897/neobiota.25.8613

Vaes-Petignat S, Nentwig W (2014) Environmental and economic impact of alien terrestrial arthropods in Europe. NeoBiota 22: 23–42. doi: 10.3897/neobiota.22.6620

Van Wilgen NJ, Wilson JRU, Elith J, Wintle BA, Richardson DM (2010) Alien invaders and reptile traders: what drives the live animal trade in South Africa? Animal Conservation 13: 24–32. doi: 10.1111/j.1469-1795.2009.00298.x

Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE, DAISIE partners (2010) How well do we understand the impacts of alien species on ecological services? A pan-European cross-taxa assessment. Frontiers in Ecology and the Environment 8: 135–144. doi: 10.1890/080083

Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. Trends in Ecology and Evolution 24: 136–144. doi: 10.1016/j.tree.2008.10.007

Wittenberg R, Cock MJW (2001) Invasive alien species: a toolkit of best prevention and management practices. CABI. doi: 10.1079/9780851995694.0000

Electronic appendix

A large number of possible combinations between pairs of individual pathways and a low number of observed species with particular pathway combinations prevented rigorous statistical testing of differences in the role of multiple pathways among taxonomic groups. Nevertheless, there was a clear trend for fishes, mammals and plants that the highest proportion of multiple pathways was associated with release and escape (intentional introductions). For terrestrial invertebrates, the highest proportion was found for the combinations "corridor and stowaways" (unintentional introductions with traded goods and their vectors without any biological meaning for the introduced species) (Table 3).

Generally, the patterns were highly taxon-specific. In fishes, most multiple pathways are associated with unaided spread. For terrestrial invertebrates where the very dominant pathway is contaminant – unaided pathway, multiple pathways are limited in frequency (Table 3). For mammals, also only few records were available and therefore only three combinations are covered, all showing high importance of intentional release and unintentional unaided spread. In plants, the combinations of several pathways are mostly associated with escape.

Table 3. Percentages and observed counts (in brackets) for pairs of introduction pathways for alien species with ecological impact among taxonomic groups. The most frequent combinations (above 3%) are highlighted. Pathways: rel – release, esc – escape, cont – contaminant, stow – stowaway, unaid – unaided.

	rel-esc	rel-cont	rel-stow	rel-corr	rel-unaid	esc-cont	esc-stow	esc-corr	esc-unaid	cont-stow	cont-corr	cont-unaid	stow-corr	stow-unaid	corr-unaid
Plants	3.9 (99)	0.4 (11)	0.2 (4)	0 (0)	0.1 (2)	1.9 (49)	0.6 (16)	0 (0)	0.3 (8)	0.5 (12)	0 (0)	0.3 (7)	0 (1)	0.2 (4)	0 (1)
Mammals	33.3 (18)	0 (0)	0 (0)	0 (0)	13 (7)	0 (0)	0 (0)	0 (0)	11.1 (6)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Fish	36.2 (38)	0 (0)	0 (0)	1.9 (2)	13.3 (14)	0 (0)	0 (0)	1.9 (2)	12.4 (13)	0 (0)	0 (0)	0 (0)	1 (1)	1 (1)	5.7 (6)
Terrestrial invertebrates	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2.7 (2)	0 (0)	0 (0)